On the Auditory and Olfactory Organs of Spiders. 329

Hab. Seychelles Islands (Dr. E. Perceval Wright).

The nearest ally of this species is *C. fusiformis*, Reeve, from which it may be distinguished by the sharper angulation of the whorls, more attenuated body-whorl, finer liration on the columella, and the slightly longer spire. The slight sinus towards the lower part of the labrum is comparatively conspicuous.

XL.—The Auditory and Olfactory Organs of Spiders. By FRIEDRICH DAHL*.

[Plate XII.]

LAST year I published, in the 'Zoologischer Anzeiger' (p. 267), a short communication upon some peculiarly articulated hairs in the Arachnida, which I interpreted as an organ of hearing. I have since continued my investigations upon this subject, as also upon the sense-organs of the spiders in general, and venture here to make known some further results.

In the first place I ascertained that the spiders have not only auditory but also olfactory perceptions, and after long seeking I succeeded in discovering in the maxillæ an exceedingly peculiar organ which, for reasons presently to be given, I think may be regarded as the olfactory organ.

But before proceeding to its description I would make some additions to the exposition of both the histological structure and the systematic significance of the auditory hairs, and also replace the indifferent woodcut representations with better drawings.

As I have already mentioned in the above-mentioned article, the auditory hairs occur upon the upper surface of the legs and palpi. I also indicated that with reference to these hairs our indigenous spiders may be divided into two groups. I have since examined, in connexion with this, nearly all the spiders that were at my disposal in a suitable state, and I can not only sustain the assertion then made, but can also make some further remarks upon the classification of the Spiders by the employment of this character.

The first group, which has been already separated upon other characters from the other spiders, I characterized as follows :—

* Translated by W. S. Dallas, F.L.S., from the 'Archiv für mikroskopische Anatomie,' Band xxiv. pp. 1-10. I. Tibia with two rows of auditory hairs, metatarsus with only one hair, and the tarsus with a cup without hairs.

Upon this it is to be remarked that the auditory hair is wanting upon the metatarsus of the fourth pair of legs*, and that one of the rows upon the tibiæ sometimes consists of only a single hair, as, for example, upon the anterior tibiæ of Erigone pusilla, Wid. The rudimentary cup upon the tarsus seems to be most characteristic of this group, and I think that a special importance must be attached to it in a natural grouping, because, as a rudimentary organ, the cup has very probably no longer a purpose to serve in the animal, and therefore directly indicates relationship. The rudimentary cup occurs in the following families :- Epeïridæ, Uloboridæ, Theridiidæ, and Pholcidæ. Of the Uloboridæ I have unfortunately been able to examine only Hyptiotes paradoxus, C. K., and even of this only a rubbed specimen, so that I recognized its belonging to this group only from the small cup just before the middle of the tarsus. The position of this family among the Orbitelariæ, which had already been selected on account of the form of the net, is completely confirmed by this character. An instinct so specially developed as the weaving of the peculiar geometric web is indeed as important as an organ, it being extremely improbable that so singular an instinct could be developed independently in different animals.

In accordance with my division into two groups, I am led to separate the genus *Phyllæca*, established by me[†], from the Agalenidæ, and to refer it to the Theridiidæ, although several other characters would seem to justify the former position.

In Pachygnatha and Tetragnatha there are auditory hairs upon the femora also, and, indeed, hitherto I have found them in this position only in those genera. They stand in two rows near the base. This fact confirms the relationship of the two genera, already deduced from other characters by Bertkau ‡. I therefore, after his example, group them together as Pachygnathidæ in the same family, and refer this to the Orbitelariæ. Thus, as in all other groups, so also among the Orbitelariæ, we should have a genus which has exchanged net-weaving for a free mode of existence. Pachygnatha further approaches the Epeïridæ also in the greater

* The genus Zilla seems to be the only exception.

† Schr. d. naturw. Ver. für Schlesw.-Holst., Bd. v. p. 61; and 'Analytische Bearbeitung der Spinnen Norddeutschlands,' Kiel (1883), p. 49.

† Bertkau, "Versuch einer natürlichen Anordnung der Spinnen," in Arch. für Naturg. (1878).

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number of the auditory hairs upon the tibiæ. There exist four in one row, whereas usually in the Theridiidæ the number three is not exceeded. *Steatoda* indeed constitutes an exception on the one side; and on the other, among the Epeïridæ, the number is less in *Singa* and *Cercidia*.

II. The tarsus not with a rudimentary auditory cup, seldom quite without auditory hairs (Dysdera), usually, as well as the metatarsus and tibia, with a considerable number. The cups in this group are much less characteristically developed.

Territelariæ.—Unfortunately of this group I had no fresh examples at my disposal, and on the spirit-specimens of the zoological collection in Kiel, which Prof. Möbius kindly made over to me for examination, the auditory hairs were for the most part broken off. So much, however, appeared to be certain, that here a considerable number of rather irregularly placed hairs exists upon the last joints of the limbs. If this be correct, the group stands in this respect in opposition to all other spiders.

The Dysderidæ are distinguished by the small number of their auditory hairs; here there exist only one or two upon the tibiæ, upon the metatarsus one, and upon the tarsus one only in *Segestria*, while there is nothing of the kind in either *Dysdera* or *Harpactes*.

In all the other families there is a considerable number of auditory hairs upon all the three terminal joints of the limbs. But according as there are one or two rows upon the tarsus, we can again distinguish two groups here :—

1. With one row of auditory hairs upon the tarsus :--Amaurobiidæ, Agalenidæ, Philodromidæ, Thomisidæ, and Attidæ.

2. With two rows of auditory hairs upon the tarsus:— Drassidæ, Anyphænidæ, and Lycosidæ. Among the Drassidæ, however, the two rows are sometimes very close together (e. g. in Prosthesima). In Argyroneta also, in which the auditory hairs in general differ less from the rest, it is difficult to say whether we have before us one or two rows.

Systematically the position of the auditory hairs, especially in the first group, may be employed much more extensively for distinguishing genera and species; but upon this I cannot here go into details.

As already mentioned, the development of the cup especially differs in completeness. Besides the character given, the first group is distinguished by the very characteristic form of this cup; hence the animals of this group are specially fitted for anatomical investigation. The cup is very fine and large in *Pachygnatha*, as shown in figs. 1 and 2 *.

The hairs usually do not stand exactly in the middle of the dorsal surface, no matter whether one or two series are present, because along the middle, immediately beneath the matrix, there runs a blood-sinus (fig. 1, bl), in which the blood flows towards the body. This is recognized in the preparation by its finely granular nature. Beneath the blood-vessel lies the main nervous cord of the leg (n), which may be pretty easily detected in the dense mass of transversely-striated muscles by its long irregularly arranged nuclei. From this main cord branches are given off to the individual hairs. If we wish to obtain a distinct picture of the course of the nerves, we must not make an exactly sagittal section, but the section must form an acute angle with the sagittal plane.

The delicate nervous branches which run to the cups are generally surrounded by pigment-grains, and thus their course is rendered particularly recognizable. The pigment accumulates especially beneath the chitinous envelope, and at the spot where the nerve passes into the main nervous cord. Before this passage the nerve is surrounded by three or four lighter ovals, as is shown in the figure, and these also are bounded by pigment-grains. The cup, the side walls of which are formed by the chitinous integument, is various in form, very shallow in the Chernetidæ, for example, and in the spiders usually more or less globular. In Pachygnatha Listeri, Sund., it is furnished with granular longitudinal costæ. At the bottom of this cup there is a second smaller cup, which projects freely from the bottom of the large one. This is filled with a finely granular substance, upon the surface of which the hair is inserted, while the nerve enters its lower part. The auditory hairs are probably never quite simple at the apex, certainly often very shortly and indistinctly plumose, but sometimes, as in the Lycosidæ, and especially in Segestria, almost pectinate. When several are present a gradual increase outwards is always shown. Rarely there is a smaller and, as it were, accessory hair between those growing regularly. When such a hair is present it is always very closely .pproximated to the neighbouring ones. When two rows are present side by side, the shorter one usually increases more rapidly in length, so that the last hairs do not differ too much in length; and this circumstance sometimes renders it possible in doubtful cases to recognize whether we have before

* In staining my preparations I employed Grenacher's hæmatoxylinsolution, which here, as in insects, gives the best nuclear staining. us one or two rows, as the hairs then are alternately larger and smaller.

The rudimentary cups upon the tarsus are usually of about the form shown in fig. 3. The connexion with the internal space is here completely cancelled. Sometimes also the upper surface is almost entirely closed, so that then there remains only a vesicle in the integument. Moreover, the hair on the metatarsus in many cases shows only a small amount of mobility, far inferior to that of the tibial hairs. Perhaps in time this hair also will meet with the same fate as the hair of the tarsus.

After the appearance of my communication in the 'Zoologischer Anzeiger' I was for a time in doubt whether the sound-waves were the *sole* adequate excitation for the auditory hairs. The ground of this doubt was furnished by the consideration, which was even then indicated, that the hairs are also fitted to convey the sensation of a puff of air. Thus, if one blows upon a Lycosid, for example, when it is slowly running along or resting quietly, it draws up the legs to the body. As it decidedly does this involuntarily, and there can be no question of an actual fright of the spider, I thought that we must recognize in this an instinctive protective arrangement of some kind. Perhaps the animal would instinctively hold fast, and at the same time present to the wind as small a surface as possible. But if I only blew as strongly as would occur at the utmost in the wind, I observed scarcely any shrinking. The strong and sudden shock of the wind would therefore have to be a painful over-excitation of the organ, and the shrinking a sign of pain. But if the hairs really serve for the perception of a breath of air, we must at the same time ascribe to them the other function of soundperception, as we are compelled to assume that every movement which is directly conveyed to the termination of a nerve is felt; and that the sound-waves set the hairs in motion may be directly observed, as has been previously stated.

The organ which I characterize as the olfactory organ is represented in figs. 4-6. Fig. 4 shows a section through the maxilla in the direction of the length of the body. In this *md* indicates the section of the maxillary gland # and *m* a muscle in section, both enclosed in connective tissue; go is the smooth anterior surface in front of which the mandibles move to and fro. This smooth hairless area on the anterior

* 'Analytische Bearbeitung,' &c. p. 18, resp. 6. Ann. & Mag. N. Hist. Ser. 5. Vol. xiv. 26 surface of the maxillæ is found, when seen under a high power from the surface, to be closely set with fine orifices. In perpendicular section (fig. 4, go) we see beneath the sieve-like integument a layer of closely approximated long cones, shown, more highly magnified, in fig. 5. Where the chitinous envelope has been slightly lifted in sectioning (as in fig. 5) these cones contract a little at the end, and in consequence they separate from each other, and thus at once show that they do not form a coherent mass.

In transverse section they exhibit a nearly regular polygonal form. Fig. 6 shows (at a) such a transverse section of the cones with the overlying integument. Here we see at once that each three or four orifices correspond to a cone. The cones consist of a finely granular mass (which reminds one of the so-called olfactory cones of the Copepoda &c.). At the bottom each of them contains a sharply defined nucleus, beneath which the cone is constricted, and seems to pass into a fine thread (fig. 5, n), which unites it to a membranous plate (pl). The cones are enclosed by an extremely delicate membrane, which emits small points into the pores of the integument. The membranous plate (pl) stretches over the whole extent of the perforated plate, and is also continued beneath the surrounding parts, where it bounds the matrix from within. A tolerably strong nerve runs to this plate; it branches off from the palpal nerve. The fine threads which run to the individual cones are therefore probably to be regarded as the final ramifications of that nerve.

If we now inquire into the origin of the organ, there can searcely be any doubt that the olfactory cones have originated from cells of the matrix. For on the one hand there is no other trace of any matrix under this part of the integument; secondly, the olfactory cells and the cells of the neighbouring matrix are in immediate contact; and, thirdly, the membranous plate, as already mentioned, is continued beneath the matrix as an inner cellular membrane.

The organ is universally distributed within the series of the Araneæ. Nevertheless it is by no means equally perfectly developed throughout. It has its finest development perhaps in *Pachygnatha*, and for this reason I have drawn my figures from preparations of this spider.

In conclusion, we have before us the question as to what function this peculiar organ may have. We might, perhaps, in the first place, think of gland-cells, and, because it is in the neighbourhood of the mouth, suppose it to be a salivary gland, although even the general form does not seem to be very much in favour of this view. But in fresh animals I found the plate always dry. I have even captured some when engaged in sucking a fly, and on examining them could not observe any trace of a fluid upon the plate.

We are therefore driven to the conclusion that it is a senseorgan, and in this conclusion we are strengthened by the presence of a strong nerve. Let us then run over the series of our senses and inquire for what sense the organ seems to be best adapted.

The sense of touch is at once excluded, because there are no projecting parts, and, moreover, the extremity of the maxillæ is abundantly furnished with tactile hairs (fig. 4, t). The position alone seems to be little in favour of its being an auditory organ, as the surface is completely concealed by the mandibles, whilst an auditory organ is usually placed as openly as possible upon the surface. Further, we have already seen reason to regard the hairs above described as organs of hearing.

The notion of an organ of taste seems to be favoured by the position on parts of the mouth. Nevertheless, as already mentioned, the porous surface remains perfectly dry during the sucking of an insect. We should therefore rather regard as taste-cells a group of cells situated on the anterior surface of the suctorial groove (which can be closed as a tube), and therefore in the labrum. These cells also receive a nerve which springs from the supra-œsophageal ganglion and runs above the œsophagus.

Thus for our organ there remains only the interpretation as an olfactory organ, unless we are inclined, without any foundation, to assume the existence of a sense that is deficient in ourselves. The position would certainly be very suitable for an organ of smell; for as the plate is covered by the mandibles, it is protected from complete desiccation. The condition that the membrane of the olfactory cells, with which the particles come into contact, must be moist, could therefore here be fulfilled.

That the sense of smell is of importance to spiders, as to all air-breathing animals, needs no proof; it is, indeed, the principal purpose of this sense to test the air that is breathed. This principal function furnishes us with a ready means of convincing ourselves of the existence of a sense of smell. The animal will instinctively avoid all strong odours. I have experimented with various species and everywhere ascertained the perception of odours. I would recommend for such experiments a species of *Erigone (E. rufipes*, Linn.), which, in this country even in winter, may be everywhere shaken out of firs and those shrubs which retain their dried leaves. This animal not only reacts very easily, but it is also particularly well adapted for the experiments on account of its behaviour. If it be placed in a covered vessel it will soon sit quietly on the wall with its legs drawn up to its body. In this position it is not easily disturbed. But if a brush dipped in oil of turpentine or oil of cloves be brought within half a centimetre ($\frac{1}{5}$ inch) of it, it regularly runs away in a few seconds. I have not been able to observe any difference of behaviour towards different odours, nor could I succeed from its actions in drawing any conclusion as to the position of the olfactory organ, the animal being too small to allow experiments to be made with this object. This, however, is certain, that spiders perceive odours; and as we find no corresponding organ in the neighbourhood of the organs of respiration, the conclusion that the organ described is actually an organ of smell may appear not inadmissible.

A priori it would seem useless to seek for histological analogies, seeing that in other Arthropods we have no more certain knowledge as to the olfactory organ; and a comparison with the corresponding organ in Vertebrata, which are constructed upon quite a different type, does not seem to be permissible. Hence we are only the more surprised that an analogy with the structure of those animals, as it were, forces itself upon us. The olfactory cells, in fact, very vividly remind us of the so-called epithelial cells in the olfactory inucous membrane of the Vertebrata. It is true that here precisely that is wanting which we there interpret as olfactory cells. This interpretation, however, is still scarcely to be regarded as demonstrated, especially as the so-called olfactory cells sometimes bear vibratile cilia, and therefore at the same time must serve another purpose. The subepithelial layer would represent the membranous plate, which here certainly does not appear to consist of cells.

In this place I may perhaps call attention to another peculiar organ of the Spiders. I call it an organ on account of its peculiar structure and its general diffusion, although I can say nothing as to its function. It occurs upon the upper surface of the metatarsus of all the legs towards the extremity, and consists, as shown in fig. 7, of a few transverse folds, some of which show dot-like enlargements. In some Theraphosidæ the outermost fold is even closely and uniformly toothed on the margins. In longitudinal sections there appears under these tolds (fig. 8) an oval, clearer mass of the matrix, which is surrounded by pigment-grains and might remind one of a nerve-termination. Hitherto, however, I have not seen any nerve-fibre running to it. Does this organ perhaps assist in any way in making the web? I have certainly never seen it employed in that operation.

EXPLANATION OF PLATE XII.

- Fig. 1. Articulation of an auditory hair in Pachygnatha Listeri, Sund. h, auditory hair (broken short); b, cup; ch, chitinous envelope; m, matrix; bl, blood-sinus; n, main nervous cord of the leg; m', a muscular fibre.
- Fig. 2. An auditory hair with its cup, from the same animal, seen from above.
- Fig. 3a. A rudimentary cup of the tarsus of the same. Fig. 3b. The same seen from above.
- Fig. 4. A longitudinal section through a maxilla of the same. m_{i} muscle, cut through: md, maxillary gland, cut through; t, a tactile bristle; go, the olfactory organ.
- Fig. 5. A part of the olfactory organ, more highly magnified. ch. perforated chitinous envelope; z, olfactory cones; n, nerve-fibres; pl, membranous plate passing under the olfactory cells.
- Fig. 6. A part of the olfactory organ from above, more highly magnified. a shows the pores of the chitinous envelope, and at the same time the transverse section of the subjacent olfactory cells.
- Fig. 7. Organ at the end of the metatarsus, seen from the surface.
- Fig. 8. The same, in longitudinal section. m, matrix; bl, blood-vessel.

XLI.—Description of a new Species of Microgale. By OLDFIELD THOMAS, F.Z.S., Natural History Museum.

IN 1882 * I had the pleasure of describing two small shrewlike Insectivores collected in Eastern Betsileo by the Rev. W. Deans Cowan, and founding for them the genus Microgale in the family Centetidæ; and I now have to add to them a third species much larger than either, and differing in several more or less important details. I propose to associate with it the name of Dr. G. E. Dobson, the author of the ' Monograph of the Insectivora,' in which work an account of the anatomy of the two original species has already appeared †.

Microgale Dobsoni, sp. n.

Colour and general appearance very much that of a large shrew. Head long and narrow, the nose produced into a long slender snout. Ears large and thin-laid forward they just cover the eye; their structure as in M. longicaudata, but their outer edge less concave. Fore feet with five well-developed toes and small equal-sized claws; fifth toes reaching to the proximal end of the terminal phalanx of the fourth. Hind

* Journ. Linn. Soc., Zool. xvi. p. 319.

† Pt. 2, pp. 86 a to e (1883).